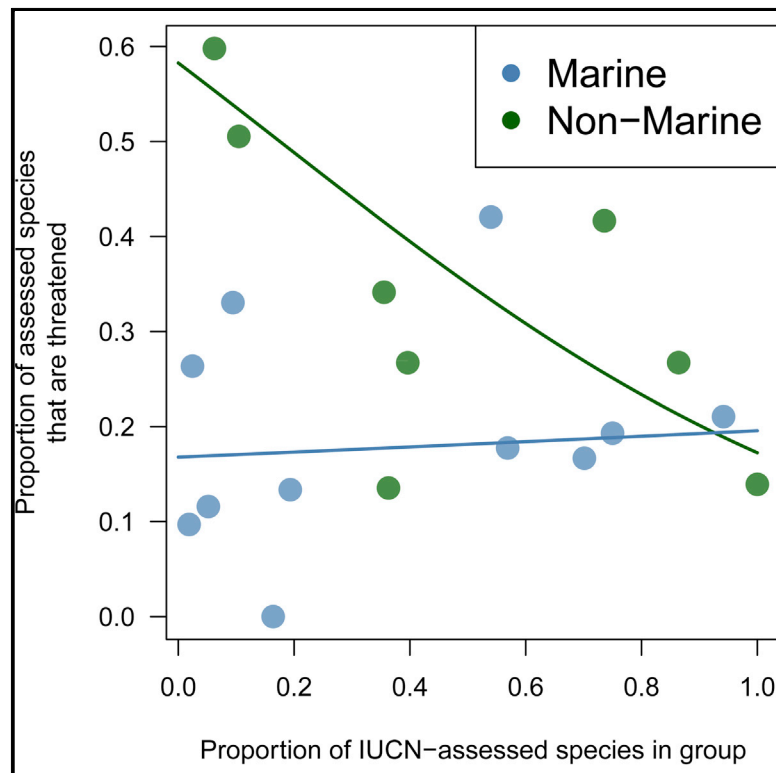


Current Biology

Global Patterns of Extinction Risk in Marine and Non-marine Systems

Graphical Abstract



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In Brief

Here, Webb and Mindel compare extinction and extinction risk globally between marine and non-marine species and show that lower rates of extinction in marine systems are at least partly explained by lower rates of conservation assessment. In the best known groups, 20%–25% of species are threatened with extinction, regardless of whether they are marine or non-marine.

Highlights

- The extinction risk of proportionally fewer marine than non-marine species is known
- Conservation assessments focus on taxonomically well-known groups in both realms
- In both realms, extinction risk increases with conservation assessment effort
- In marine and non-marine taxa, between 20% and 25% of species are at risk of extinction



Global Patterns of Extinction Risk in Marine and Non-marine Systems

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Summary

Despite increasing concern over the effects of human activities on marine ecosystems [1, 2], extinction in the sea remains scarce: 19–24 out of a total of >850 recorded extinctions [3, 4] implies a 9-fold lower marine extinction rate compared to non-marine systems. The extent of threats faced by marine systems, and their resilience to them, receive considerable attention [2, 4–6], but the detectability of marine extinctions is less well understood. Before its extinction or threat status is recorded, a species must be both taxonomically described and then formally assessed; lower rates of either process for marine species could thus impact patterns of extinction risk, especially as species missing from taxonomic inventories may often be more vulnerable than described species [7–11]. We combine data on taxonomic description with conservation assessments from the International Union for Conservation of Nature (IUCN) to test these possibilities across almost all marine and non-marine eukaryotes. We find that the 9-fold lower rate of recorded extinctions and 4-fold lower rate of ongoing extinction risk across marine species can be explained in part by differences in the proportion of species assessed by the IUCN (3% cf. 4% of non-marine species). Furthermore, once taxonomic knowledge and conservation assessments pass a threshold level, differences in extinction risk between marine and non-marine groups largely disappear. Indeed, across the best-studied taxonomic groups, there is no difference between marine and non-marine systems, with on average between 20% and 25% of species being threatened with extinction, regardless of realm.

Results

Across All Species, Rates of Extinction Are Higher in Non-marine Species

Rates of taxonomic description, International Union for Conservation of Nature (IUCN) assessment, extinction, and extinction risk for 226,101 marine and 1,463,813 non-marine species are summarized in Figure 1. Based on estimates of taxonomic completeness for the focal taxonomic groups [10, 12, 13], a similar proportion of all marine (27%) and non-marine (28%) species have been described. These estimates are highly uncertain, but the similarity between marine and non-marine groups agrees with previous analyses of smaller sets of species [13]. The IUCN lists 20 described marine species as recently extinct (0.009%) and 1,206 (0.53%) as threatened with extinction. Rates of extinction (0.057%) and threat (1.37%) are, respectively, 6.42× and 2.60× higher per described non-marine species. This discrepancy is in part due to the fact that only 3.02% of described marine species

have been IUCN assessed, cf. 3.61% of described non-marine species. Extinction and threat rates per assessed species are 0.29% and 17.49% for marine species, respectively, 5.4× and 2.2× lower than the rates for non-marine species (1.57% and 38.00%; Figure 1).

Fewer Marine Species Occur in Well-Described, Well-Assessed Taxonomic Groups

IUCN assessments are disproportionately focused on species within the 19 marine and ten non-marine groups that we define as taxonomically well described. A total of 63.8% of assessed marine and 87.9% of assessed non-marine species occur in these groups (Table 1 and Figure 2), which also include most of the recorded extinctions (70.0% of marine and 89.9% of non-marine) and current threatened species (54.3% of marine and 87.0% of non-marine). Importantly, more non-marine than marine species occur within well-described groups, in absolute numbers (406,778 in ten non-marine groups cf. 38,011 in 19 marine groups; Table 1), proportions of described species (27.8% non-marine cf. 16.8% marine), and proportions of predicted total species numbers (10.0% non-marine cf. 5.2% marine).

We define 11 marine and eight non-marine groups as well assessed by the IUCN (of which six and seven, respectively, are also well described; Table 1). These contain 42.7% of all described and 98.8% of all assessed marine species and 25.5% of described and 96.9% of assessed non-marine species. These well-assessed groups contain substantially more described non-marine (372,724) than marine (96,651) species.

Apparent Threat Increases with Conservation Assessment in Both Realms

Across well-assessed groups, the proportion of *described* species listed as threatened or extinct increases with the proportion of IUCN-assessed species in both marine and non-marine taxa (Figure 3A). The relationship differs across realms (binomial generalized linear model, significant interaction between P(assessed) and realm, $z = -18.77$, $p < 0.0001$), but differences between realms—particularly at higher values of P(assessed)—are relatively minor compared to differences within realms. Precise predictions are unwise as our model does not attempt to explain differences in “true” threat rates (at 100% assessment) between groups; however, threatened species accumulate faster as more species are assessed in the marine realm, such that the lines for the two realms cross when ~80% of species within a group are IUCN assessed (Figure 3A). At this level of assessment, 15%–25% of described species are predicted to be threatened or extinct regardless of environment.

The proportion of assessed species that are threatened or extinct (P(threatened, extinct | assessed)) in these groups (Figure 3B) is also related to the proportion assessed, with clear differences between realms (significant interaction between P(assessed) and realm, $z = -16.7$, $p < 0.0001$), consistent with assessment efforts focusing on at-risk species first in non-marine, but not in marine, groups. Considering only those groups in which P(assessed) is high enough for this discrepancy to lessen (more than one-third of described species assessed), the proportion of assessed species that

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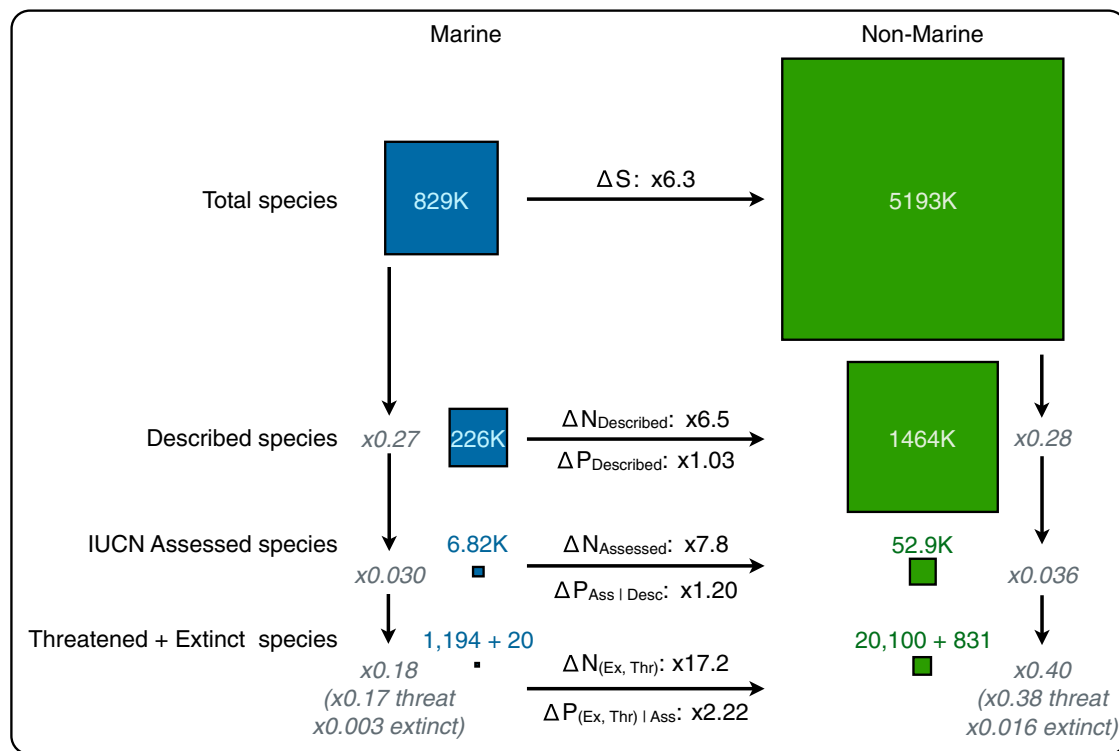


Figure 1. Differences in Numbers of Total Species, Described Species, IUCN Assessed Species, and Threatened and Extinct Species, between Marine and Non-marine Taxa

This figure is based on the >99% of described marine species and the large fraction of described non-marine species present in the 88 marine and 19 non-marine groups included in our dataset. The area of each box is proportional to the number of species it represents. Numbers along the horizontal arrows give differences (Δ) between realms as non-marine numbers (N) and proportions (P) as a multiple of the marine figure. For instance, the number of described species in the non-marine realm that have been IUCN assessed is around 8 \times higher than the in the marine realm ($\Delta N_{\text{assessed}} \times 7.8$), but the difference between realms in the proportion of described species that have been assessed is rather smaller (the difference in proportions assessed given described, $\Delta P_{\text{Ass} | \text{Desc}} \times 1.20$). Vertical arrows give the number of species within a realm as a proportion of the numbers in the level immediately above it (e.g., “ $\times 0.030$ ” indicates that around 3% of described marine species have been assessed by the IUCN).

are threatened or extinct is similar (and similarly variable) in marine (mean \pm SD: 0.23 ± 0.106 , $n = 5$) and non-marine (0.26 ± 0.111 , $n = 6$) groups. Regardless of realm, in groups for which estimates of extinction rates are likely to be most robust, on average 20%–25% of IUCN-assessed species are extinct or at risk of extinction.

Discussion

The oceans have a habitable volume 600 \times larger than the terrestrial biosphere [14]. This vast realm is mostly inaccessible to us, which leads to the assumption that human-driven marine extinctions are unlikely. Superficially, the IUCN data bear this out: according to our criteria, only 20 marine extinctions have been recorded across just six of the 88 marine taxonomic groups that we consider (six seabirds, five fish, four gastropod mollusks, three marine mammals, one nemertean worm, and one red alga), within the range of previous estimates [4, 5]. Similar discrepancies occur within groups occurring in both realms: extinction of 1.8% of non-marine mollusks is a rate >250 \times that observed in marine mollusks (0.007%) [15], and although similar numbers of fish species occur in marine and freshwater habitats [16], >10 \times more freshwater ($n = 66$) than marine ($n = 5$) species have been recorded as extinct.

However, anthropogenic activities are pervasive and are increasing throughout the oceans [2, 17–20], and so determining

whether marine extinctions are truly unlikely or simply hard to detect is important. We show that differences between realms in observed rates of extinction and extinction risk are at least partially explained by differences in the degree to which species have been described and assessed. In particular, extinction risk is similar in marine and non-marine systems in the best-known taxonomic groups, i.e., those that have been both well described taxonomically and well assessed by the IUCN (Figure 3). This is supported by previous work on individual taxonomic groups revealing high levels of threat within certain marine taxa: 30% of seabirds [21], 33% of reef building corals [22], and at least 25% of sharks and rays [23] are at an elevated risk of extinction, rates comparable with non-marine groups widely considered to be highly threatened (e.g., 33% of amphibians [24]).

These results suggest the arguments that marine species possess “extinction resistance” traits such as high fecundity, large ranges, and high dispersal ability [25–28] are overly simplistic and neglect much variation within each realm [29]. For instance, although some marine species have large ranges, most do not: just as on land, rarity is the norm in marine systems [11, 29, 30]. Equally, supposed “extinction resistance” traits may not actually confer low risk of extinction: species with high dispersal potential can exhibit genetic differentiation over small scales [31, 32] or be tied to specific sites (and thus potentially vulnerable) for large parts of their lives

Table 1. Numbers of Total, Described, and IUCN-Assessed Species in Well-Described and Well-Assessed Groups of Marine and Non-marine Species

Realm	Taxon	Rank	Number of Species					P _{threat assessed}
			Total	Known	Assessed	Threatened	Extinct	
M	<i>Branchiopoda</i>	class	90	90	1	0	0	0
M	<i>Phoronida</i>	phylum	18	18	0			
M	<i>Mangroves</i>	other	78	75	57	11	0	0.19
M	<i>Mammalia</i>	class	140	135	88	34	3	0.42
M	<i>Hexapoda</i>	other	2,147	2,037	1	1	0	1
M	<i>Seagrasses</i>	other	73	68	54	9	0	0.17
M	<i>Hemichordata</i>	phylum	128	118	0			
M	<i>Aves</i>	class	721	641	613	123	6	0.21
M	<i>Polyplacophora</i>	class	1,055	930	0			
M	<i>Crinoidea</i>	class	723	623	0			
M	<i>Thaliacea</i>	class	92	79	0			
M	<i>Myxozoa</i>	phylum	3,261	2,686	0			
M	<i>Reptilia</i>	class	135	110	62	11	0	0.18
M	<i>Echiura</i>	phylum	218	175	0			
M	<i>Foraminifera</i>	phylum	7,500	6,000	0			
M	<i>Merostomata</i>	class	5	4	1	0	0	0
M	<i>Asteroidea</i>	class	2,434	1,922	0			
M	<i>Pisces</i>	other	21,733	16,733	3,476	459	5	0.13
M	<i>Ophiuroidea</i>	class	2,769	2,064	0			
M	<i>Anthozoa</i>	class	8,318	5,230	678	224	0	0.33
M	<i>Cephalopoda</i>	class	1,411	761	163	0		
M	<i>Holothuroidea</i>	class	3,683	1,683	95	11	0	0.12
M	<i>Gastropoda</i>	class	127,000	32,000	640	58	4	0.10
M	<i>Malacostraca</i>	class	204,234	29,748	816	215		
N	<i>Aves^a</i>	class	9,279	9,349	9,380	1,177	128	0.26
N	<i>Mammalia</i>	class	5,360	5,352	4,625	1,160	76	0.14
N	<i>Mantodea</i>	suborder	840	792	3	1	0	0.33
N	<i>Orthoptera</i>	order	26,700	23,541	28	21	1	0.79
N	<i>Reptilia</i>	class	9,865	8,624	3,418	891	22	0.27
N	<i>Odonata</i>	order	6,200	5,416	1,966	265	1	0.14
N	<i>Pisces</i>	other	18,267	14,536	5,165	1,697	66	0.34
N	<i>Tracheophyta</i>	division	368,050	281,621	17,568	10,381	124	0.60
N	<i>Mollusca</i>	phylum	54,003	41,311	4,320	1,863	320	0.51
N	<i>Bryophyta</i>	division	22,750	16,236	41	35	2	0.90
N	<i>Amphibia</i>	class	15,000	6,515	4,794	1,961	36	0.42

Realm is M for marine and N for non-marine groups. Total is the midpoint of estimates of total species richness for each group; known is the total number of described species, assessed is the number assessed by the IUCN (not including Data-Deficient species), and threatened and extinct are those assigned to the relevant IUCN categories. P_{threat | assessed} is the proportion of assessed species listed as either threatened or extinct. Groups are sorted within realm in descending order of the proportion of total species that are known. Well-described groups are in italics, and well-assessed groups are in bold. Groups illustrated in Figure 3B are identified by the first three letters of their name, underlined here. Figures for all taxa, including poorly described groups, are available in Table S1.

^aThe number of described non-marine bird species is higher than the estimated total number of species because of variation in estimated species numbers between sources. Likewise, the number of assessed bird species exceeds the number of described species, most likely due to synonymy within the IUCN database. We therefore assume that all non-marine bird species are known, and that all have been assessed by the IUCN. Minor variations around this figure will not affect our conclusions.

[33], and high fecundity does not predict how well marine fish populations recover after overexploitation [34]. There is little empirical support for a priori expectations of high levels of intrinsic extinction resistance in marine species.

Marine groups that have been well assessed by the IUCN are, however, primarily coastal, dependent on terrestrial habitats for crucial parts of their lifespans, or air breathing, and it could be argued that these groups have more regular contact with humans than is typical of marine taxa, although it is not obvious that this should lead to a higher risk of extinction compared with other, less conspicuous taxa occurring in similar environments, for example *Conus* gastropods [35]. Such groups are also typically less speciose in the sea than on land, with 15× fewer seabird species and 40× fewer marine mammal species than non-marine members of the same groups. This paucity of marine species in charismatic groups may contribute to the overall lack of marine assessed species. In contrast, we know next to nothing about extinction risk in many marine taxa: 73% of the 88 groups that we consider

here (Table S1), constituting 31% of all known marine species, have had no assessments at all. Finally, considerable controversy exists over applying IUCN criteria to some marine taxa, especially commercially fished species [36, 37], suggesting that extinction risk may be underestimated in some groups.

Two other factors may also lead to underestimation of marine extinction risk. First, rates of “Data-Deficient” (DD) IUCN classifications in marine taxa (28.6%; 2,730 of 9,554 assessed species) are double those in non-marine taxa (14.7%; 9,365 of 63,909 species). DD species often have ecological and life history traits that lead to a high likelihood of being threatened [11, 23, 38–40], suggesting that improved knowledge of marine taxa is likely to increase the number of documented extinct and threatened species. Such efforts are challenging because species poorly known in one respect (e.g., their geographic distribution) also tend to be poorly known in others (e.g., their biological traits [41]). Second, Figure 3B suggests that non-marine assessment efforts may target the most vulnerable members of a taxonomic group first, whereas no such trend

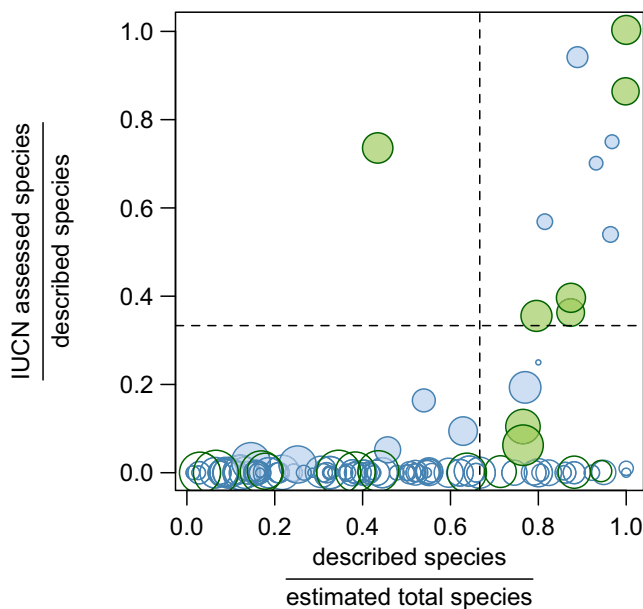


Figure 2. Conservation Assessment Has Been Focused on Well-Known Groups in Both Marine and Non-marine Realms

Here, the proportion of described species within each of the 88 marine and 19 non-marine groups included in our dataset that have been assessed by the IUCN is plotted as a function of the estimated level of taxonomic knowledge for each group (number of described species over estimated total species richness). Marine groups are shown in blue and non-marine groups in green, and the size of each point is proportional to the number of described species in each group. Solid symbols represent those groups that we consider either taxonomically well described (the proportion of known species exceeds two-thirds [vertical dashed line]) or which have been well assessed by the IUCN (the proportion of assessed species exceeds one-third [horizontal dashed line] or the number of assessed species exceeds 90 and this constitutes $\geq 1\%$ of species in the group). In general, the conservation status of large proportions of described species is known only for those groups in which taxonomic knowledge is high (i.e., most species have already been described). Amphibians (non-marine) are the clear outlier, with around 75% of known species having been assessed, despite estimates that only around 40% of all species have yet been described—a testament to their high conservation priority. See also Figure S1.

is discernable in the marine realm. It makes sense to target first taxa likely to be at risk, but this further complicates comparisons across realms.

We find little evidence for differences in global extinction risk between marine and non-marine taxa, with approximately 20%–25% of species within a group being at risk of extinction in both realms (Figure 3B). This comparison is based on the assumption that a robust estimate of extinction risk within a taxonomic group requires both a high level of taxonomic description (as the species described first within any group are typically those which are most common and least likely to be threatened) [10] and considerable conservation assessment effort within those groups. Further effort is needed to test whether these results are representative of all taxa, and thus whether 20%–25% species are indeed threatened with extinction across realms, regardless of estimates of total species number. The paucity of recorded marine extinctions does however suggest that the threat to marine species may not yet be sufficiently great to force many to extinction, in part because the geographic scale of human activities in the seas has increased markedly only in the last century [19]. This buys time to implement conservation efforts before species

are lost [42], yet the loss of marine populations is already common [4], and so the lack of recorded global extinctions is not cause for complacency. Rather, it should spur us on to trying to achieve a better understanding of the species that inhabit our oceans and the threats that they face, taking action to increase rates of taxonomic description and assessment of extinction risk [42] in order to prevent a biodiversity crisis in the oceans as severe as that on land.

Experimental Procedures

Species Lists and Taxonomic Description Rates

We assembled lists of species occurring within taxonomic groups for which estimates of both described and undescribed species numbers are available. We grouped species into 88 major eukaryotic marine taxonomic groups listed in [12] (see the Supplemental Experimental Procedures for details), which together include 226,101 valid marine species names (>99% of all valid marine species in the World Register of Marine Species, WoRMS; [43]). We calculated for each group the proportion of species described, using the number of known species and the midpoint of the minimum and maximum number of total species [12], which results in an estimated total 828,756 marine species (Table S1). There is uncertainty around estimates of total species across all groups (698,918–958,593) and within each taxon, but the groups that are well described on which we focus most attention typically have lower ranges of estimated total species (see the Supplemental Experimental Procedures and Figure S1). Non-marine data are based on estimates of the completeness of description for 19 groups of various ranks [10,13] (see the Supplemental Experimental Procedures). Our final list includes 1,463,813 non-marine described species and 5,192,742 estimated total species (Table S1). There is no comprehensive list of all valid non-marine described species, but some estimates are as low as ~ 1 million species [44], so we are confident that our list constitutes a large fraction of all described non-marine eukaryotes. In both realms, we define “well-described” groups as those in which at least two-thirds of the estimated total number of species have already been described (Table 1).

Estimates of Extinctions and Extinction Risk

We extracted the full list of 73,686 species assessed by the IUCN [3] (search URL <http://www.iucnredlist.org/search/link/53a02f68-f6a97179>, accessed June 2014) and matched it to the full list of 431,871 names (including synonyms and unaccepted names) occurring in WoRMS [43] at the “species” rank. Further details, including definitions of marine species and procedures for dealing with taxonomic disagreements between sources, are given in the Supplemental Experimental Procedures. A total of 97% of species on the IUCN list were assigned to one of the taxonomic groups listed in Table S1, totaling 9,554 marine species and 61,664 non-marine species.

Species classified as DD by the IUCN have undergone a formal assessment process; however, we consider such species to be too poorly known to contribute usefully to our analysis of extinction risk, and so hereafter we use “assessed” to refer only to the 6,824 marine and 54,544 non-marine species in our dataset that have an IUCN category other than DD. The rate of DD assessments in marine taxa (28.5%; 2,752 of 9,659 species) is double that in non-marine taxa (14.7%; 9,365 of 63,909 species), which has important implications for extinction risk assessments (see the Discussion).

Distribution of Extinct and Threatened Species across Taxonomic Groups

We summarize the number of extinct and threatened species in marine and non-marine environments as proportions of all described and all IUCN-assessed species, defining extinct species as all those classed as EX (extinct) or EW (extinct in the wild) and threatened species as those falling into any of CR, EN, or VU (critically endangered, endangered, or vulnerable, respectively). All other (non-DD) assessed species are not considered to be at risk of extinction. We estimate the extent to which IUCN assessments are concentrated in taxonomically well-described groups and consider how the relative richness of these taxonomically well-known groups differs between realms.

Cross-realm Analyses of “Well-Assessed” Groups

We define “well-assessed” groups as those in which at least one-third of described species have been assessed by the IUCN, or in which at least

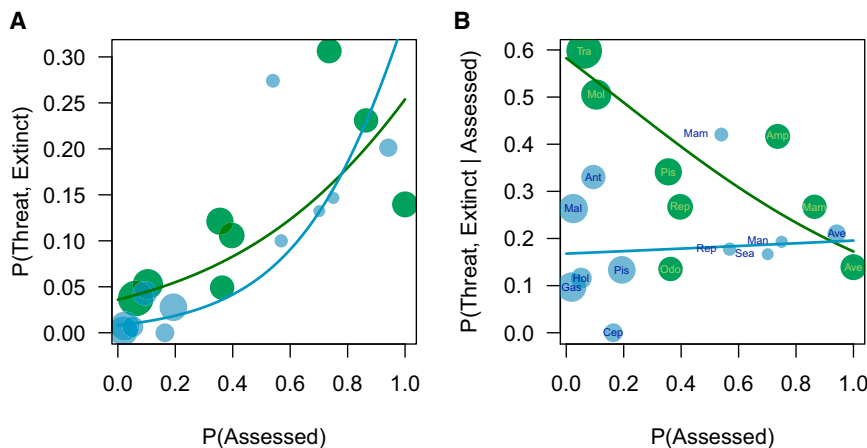


Figure 3. Conservation Concern Varies with Conservation Assessment Effort in Both Marine and Non-marine Taxa

(A) Across only those groups that have been well assessed by the IUCN, the proportion of species that are either extinct or threatened with extinction is higher in groups with higher proportions of assessed species. The lines show the fit of a binomial GLM of the proportion of threatened or extinct species within a group, $P(\text{threat, extinct})$ as a function of the proportion IUCN-assessed, $P(\text{assessed})$, realm, and their interaction. In both realms, total threat rates for a group are expected to be around 20% of described species once around 80% of described species have been assessed.

(B) The proportion of IUCN-assessed species only that are threatened or extinct ($P(\text{threat, extinct} | \text{assessed})$) also varies with the proportion of assessed species.

tion of species within a group that have been assessed ($P(\text{assessed})$; solid lines indicate binomial GLM of $P(\text{threat, extinct} | \text{assessed})$ on $P(\text{assessed})$, realm, and their interaction). At low values of $P(\text{assessed})$, non-marine groups (green symbols) tend to have a higher apparent threat rate than marine groups (blue symbols). However, once $P(\text{assessed})$ exceeds one-third, this difference between the realms disappears, with between 20% and 25% of assessed species in a group likely to be threatened or extinct regardless of realm. Labels identify taxonomic groups by the first three letters of their names, underlined in Table 1.

90 species have been assessed and where this figure represents $\geq 1\%$ described species in the group. These criteria rank groups such as Tracheophyta (non-marine, 17,568 of 281,621 species assessed) and Gastropoda (marine, 650 of 32,000 species assessed) as well assessed but not groups such as Merostomata, in which one of only four described species has been assessed. Across these well-assessed groups, we test whether the relationship between the proportion of threatened or extinct species $P(\text{threatened or extinct})$ and the proportion of assessed species $P(\text{assessed})$ differs between the marine and non-marine realms. We fit a binomial generalized linear model of $P(\text{threatened or extinct})$ as a function of $P(\text{assessed})$, realm (marine or non-marine), and their interaction. Finally, we test across well-assessed and well-described groups for a difference between realms in the proportion of assessed species that are threatened or extinct—that is, threat and extinction rates per assessed species, $P(\text{threatened, extinct} | \text{assessed})$ —and whether this varies across groups differing in their levels of conservation assessment. We fit a binomial GLM of $P(\text{threatened, extinct} | \text{assessed})$ as a function of $P(\text{assessed})$, realm, and their interaction. Both models are designed to test for general differences in extinction risk between marine and non-marine groups in which taxonomic and assessment effort are similar. All data manipulation and statistical analyses were performed in R 3.0.2 [45], and data and code are available on figshare (data: <http://dx.doi.org/10.6084/m9.figshare.1258968>; code: <http://dx.doi.org/10.6084/m9.figshare.1258984>).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.12.023>.

Author Contributions

T.J.W. and B.L.M. designed the study and created the dataset, T.J.W. analyzed the data and created the figures, and T.J.W. and B.L.M. wrote the manuscript.

Acknowledgments

T.J.W. is a Royal Society University Research Fellow. B.L.M. gratefully acknowledges the financial support provided by the Leonard Eastham Prize awarded to an undergraduate from the Department of Animal and Plant Sciences, University of Sheffield for academic merit. We thank all the contributors to the IUCN assessments of marine and non-marine species. We thank Ward Appeltans, Bart Vanhoorne, and the World Register of Marine Species for assistance with assembling the marine taxonomic data. Thanks to Rob Freckleton and Julia Blanchard for discussion and to anonymous reviewers for valuable comments.

Received: July 15, 2014

Revised: October 10, 2014

Accepted: December 9, 2014

Published: January 29, 2015

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